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THE MECHANISM OF AUTOTOMY IN *LACERTA*

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*Introduction*

Many lizards have a special mechanism for breaking off their tails as a means of escape from enemies, the process being known as autotomy (self-mutilation). As a rule the break occurs at one of a series of predetermined planes of weakness which are distributed along the greater part of the tail, one of these fracture planes passing through each of the caudal vertebrae and surrounding tissues. Fracture planes are absent in the base of the tail which contain the first six or more vertebrae; this region is close to the reproductive organ so that autotomy here would not be desirable.

The structure of the fracture planes has been described by various authors; among the most important accounts are those by Woodland (1920) of the gecko *Hemidactylus*, and by Pratt (1946) and Quattrini (1952a, b; 1953, 1954) of lacertids. Etheridge (1967) has described variations in the arrangement of the bony fracture planes in a wide range of saurian groups. Nevertheless, certain points, in particular of the muscular system, still require clarification and interpretation along functional lines.

Except when stated otherwise, our anatomical observations refer to the mid-caudal region of *Lacerta vivipara*, of which skeletal preparations and serial sections stained with Masson's trichrome, Van Gieson, and haematoxylin and eosin were available. We have also filmed 24 induced autotomies in 6 specimens of the Madeira wall lizard (*Lacerta dugesii*) at ambient temperatures of 30-35°C.

FRACTURE PLANES AND CAUDAL ANATOMY OF *LACERTA VIVIPARA*

1. THE VERTEBRAE

The vertebral fracture planes have been well described by Pratt. Each plane is represented by a split which divides the vertebrae into anterior and posterior portions, the anterior being slightly shorter (Figs. 1, 2). The split divides the centrum, where its edges are bordered by conspicuous bony ridges or "lips", and continues dorsally through the neural arch on each side; it then extends up into the anterior neural spine but stops just short of the tip. The split passes mainly behind the single transverse process on each side, but passes obliquely through the posterior part of the base of the process. In some sections periosteal connective tissue can be seen within the margins of the split. A few cartilage cells can sometimes be seen embedded in the bony lips of the split, but we can find no distinct septum or ring of cartilage (or of other material) within the split as some workers have described.

2. THE AUTOTOMY SEPTUM, SKIN, AND SEGMENTATION OF THE TAIL

The vertebrae of the tail are surrounded by a layer of fat, and outside this again are the muscles and the skin. Both fat and muscles are subdivided by a number of septa or sheets of connective tissue (Fig. 3D). The autotomy septum will be described first; the other septa are more conveniently dealt with along with the muscles and fat.

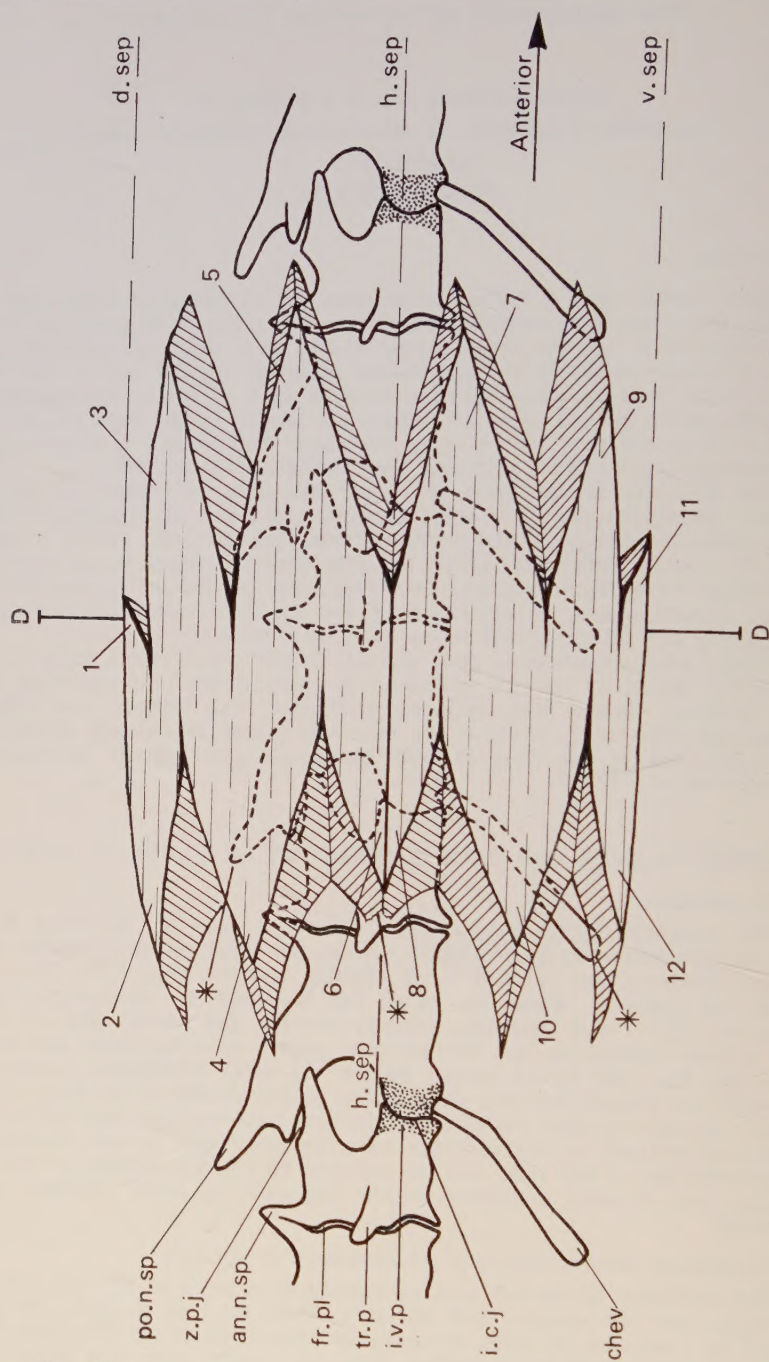


Fig. 1

The autotomy septum arises from the margins of the vertebral split, where it blends with the periosteum, and continues the plane of fracture outwards across the soft tissues towards the skin. It is perforated in the midline beneath the vertebra by the caudal artery and vein and does not cross the vertebral canal.

Although the outline of the autotomy septum conforms with the complex interlocking arrangement of the muscles, it lies essentially in the transverse plane of the tail. Consequently these septa demarcate a series of autotomy segments throughout the tail, except for the basal region. Each autotomy segment includes a muscle segment or myomere, a segment of fat, and the rear part of one vertebra together with the front part of the vertebra behind it. This arrangement corresponds with the segmental pattern of embryonic development. Each vertebra is derived from parts of two adjacent segments, and the autotomy septum and split in the vertebra represent the site of the primitive intersegmental boundary (see Werner, 1971).

The caudal scales are segmentally arranged, there being two transverse scale rows to each autotomy segment. The scales of the front row of each segment are shorter in antero-posterior length than those of the back row, and at autotomy the split in the skin occurs through the scale hinges at the front of a short row and behind a long row (Quattrini, 1952a). This point corresponds approximately with the split in the vertebra and is a useful guide in experiments which involve amputation of the tail.

The autotomy septum appears to end by blending with the deep layer of the dermis. Previous authors have described modifications for autotomy in the dermis of various lizards, including *Lacerta sicula* (Quattrini, 1954). In some of our material of *L. vivipara* the middle layer of the dermis beneath the appropriate scale hinges shows a localised condensation of connective tissue (Fig. 2). The junction between this and the looser adjacent tissue may provide a plane of cleavage.

### 3. THE MUSCLES, FAT AND LONGITUDINAL SEPTA

The muscles of the autotomous part of the tail have a complicated arrangement which is not easy to describe. Each muscle segment, together with the segment of fat which it surrounds, is divided into four portions, easily recognisable in transverse section (Fig. 3D). Thus, on each side of the tail there is one epaxial muscle and fat band, and similar hypaxial structures; these are separated by a horizontal longitudinal septum. This septum is attached along its inner edge to the length of the vertebra in the region where centrum and neural arch merge, and to the transverse process. Like the median septa it ends at the deep aspect of the dermis.

Each epaxial and each hypaxial muscle and fat band is separated from its fellow of the opposite side by a part of the longitudinal median septum. The dorsal part of this, between the epaxial tissues, arises from the dorsal midline of the vertebra, including the anterior and posterior neural spines.

The ventral median septum which separates the hypaxial structures is bilaminar, each layer arising from the centrum and intervertebral pad slightly to one side of the midline (Fig. 3D). The two layers of this septum enclose the caudal artery and vein and are attached to the two limbs of the V-shaped chevron bone. Where this septum lies between the ventral fat bands it encloses a smaller band of fat between its layers.





Fig. 2

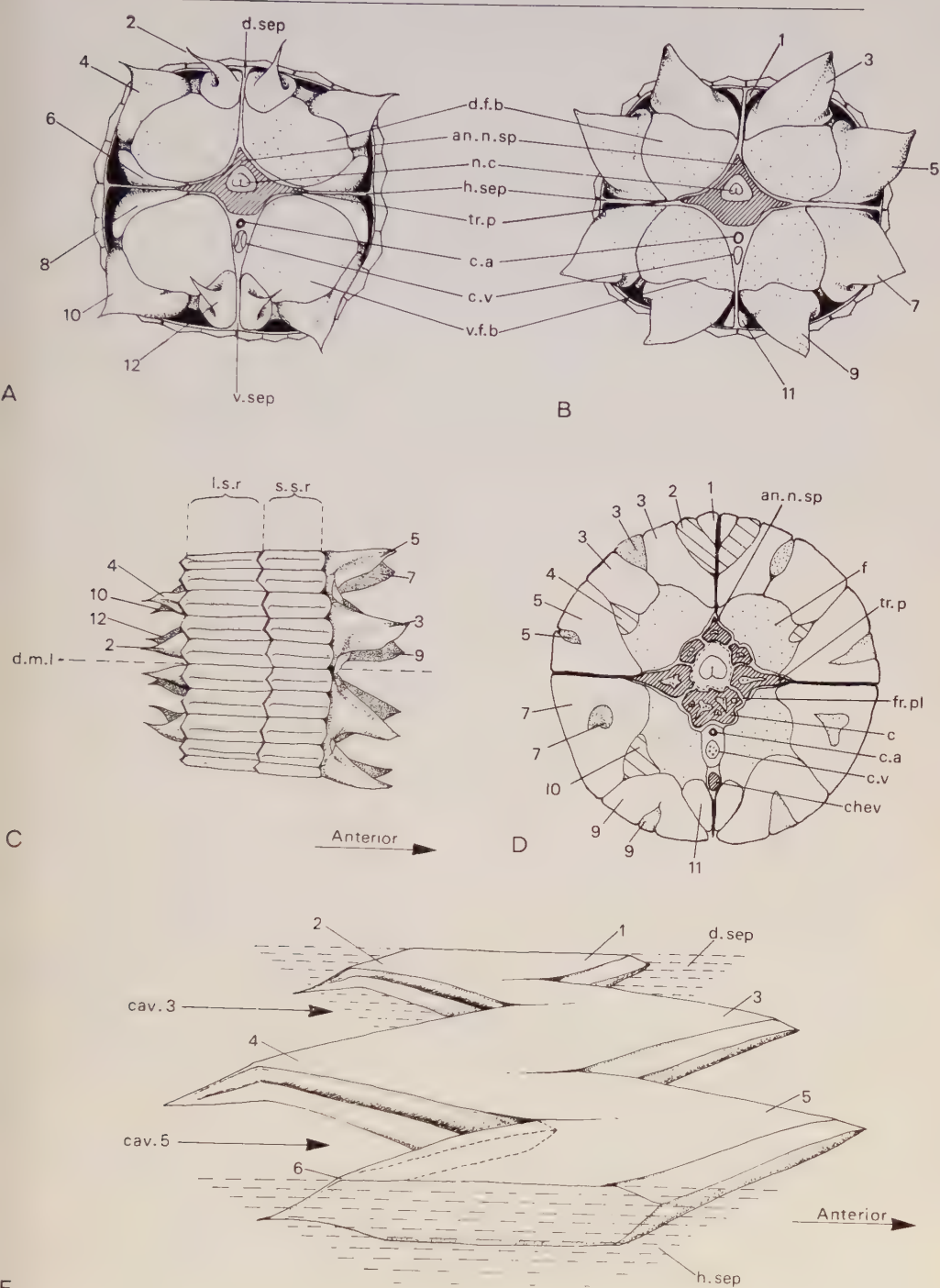


Fig 3

Each epaxial and each hypaxial muscle has three (dorsal, middle and ventral) pointed processes in front (designated by odd numbers in Fig. 1), and three behind (even numbers). These interlock with the corresponding processes of adjacent muscles and enclose recesses in which the tips of the latter are lodged (Fig 3C, 3E). The processes of each muscle are partly separated from each other by bands of connective tissue, and are separated from those of the muscles of adjacent segments by the autotomy septum. The anterior dorsal processes of each epaxial muscle (1) and the anterior ventral processes of each hypaxial muscle (11) are smaller than the rest.

Because of the interlocking arrangement the muscle blocks seen in transverse section may be derived from two or more segments (Fig. 3D).

Superficially the muscles are attached to the dermis. Their deep surfaces are mainly in contact with the fat bands, but are attached to the vertebrae in certain places, either directly or through the medium of septa. These attachments are as follows:

(a) The dorsal parts of the epaxial muscles (2) on each side are attached to the posterior neural spine, both directly and via the dorsal median septum.

(b) A small slip of muscle fibres arises from the deep aspect of the posterior middle epaxial process (4) and is attached to the capsule of the zygapophysial joint by means of a fibrous band.

(c) The posterior ventral epaxial process (6) is directly attached to the front of the transverse process of the vertebra.

(d) The posterior dorsal hypaxial process (8) is also attached to the front of the transverse process.

(e) The posterior ventral hypaxial process (12) is attached to the tip of the chevron.

As Woodland (1920) and Quattrini (1952b) have pointed out, only the posterior processes of the muscles have firm bony attachments. Each anterior process extends into the recess between the posterior processes of the muscle in front and is attached only to the autotomy septum. At autotomy separation will therefore take place only at this anterior and weaker attachment.

Immediately after autotomy has occurred, four pairs of anterior muscle processes can be seen projecting conspicuously from the front of the detached portion of tail (3, 5, 7, 9 in Figs. 1 and 3B, 3C). The processes 1 and 11 in Fig. 1. do not project from the tail fragment.

The broken surface of the stump shows four pairs of recesses which, before autotomy, accommodated the anterior processes of the tail fragment. These recesses lie between the posterior processes of the muscles in front (Figs. 3A, 3E). The latter project beyond the broken skin of the stump to some extent, though they are less prominent than the anterior processes on the fragment and seem to have been overlooked by most workers. Soon after autotomy they appear to shrink and become hidden by the contraction of the skin around the stump surface. We confirm Quattrini's observation (1954) that after breakage the autotomy septum adheres to the posterior processes. The septum may therefore protect the muscles of the stump from injury; this helps to explain the finding that muscle cells make no substantial contribution to the blastema from which the regenerating tail is formed (see Bryant, 1970).

#### 4. THE SPINAL CORD AND BLOOD VESSELS

The spinal cord is slightly constricted in the region of each vertebral fracture plane, the constriction being more marked in the lateral plane than dorso-ventrally.

Quattrini (1954) was unable to find sphincters in the wall of the caudal artery of *Lacerta sicula*. In *L. vivipara*, however, the walls of this artery show a series of elongated regional thickenings. Each of these starts just behind the level of the vertebral split and extends forwards as far as the front of the



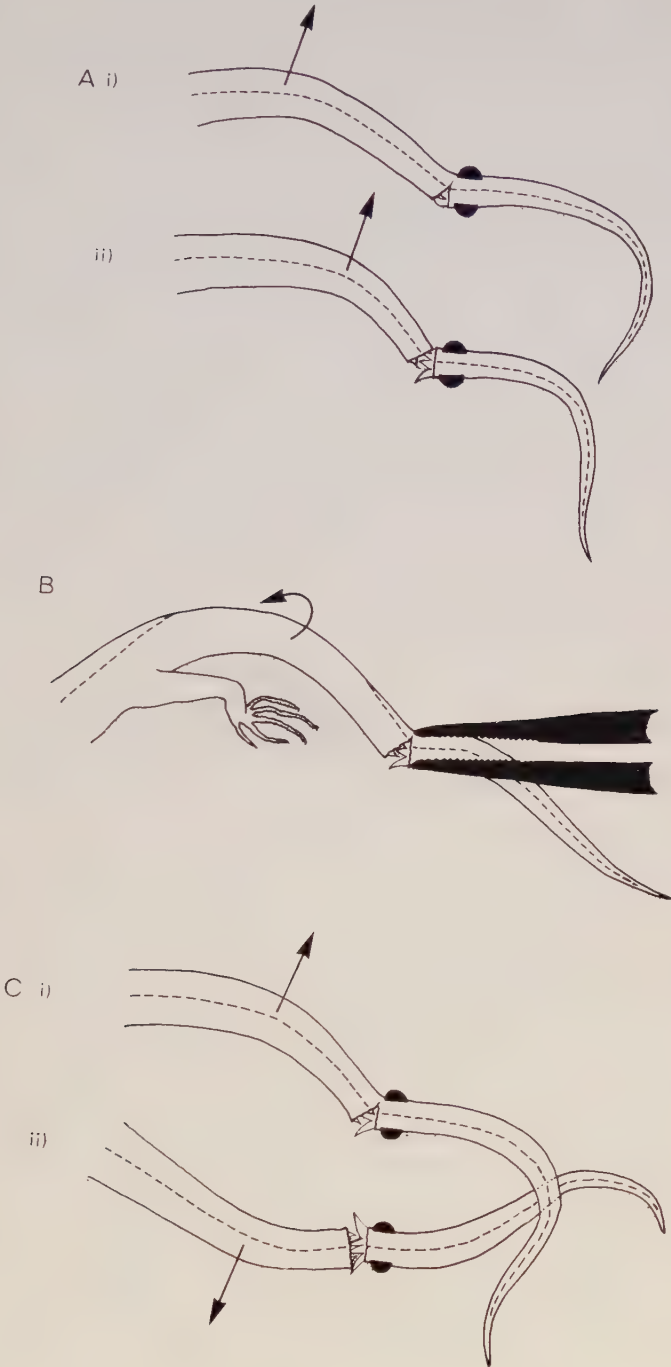


Fig. 4

same vertebra, therefore occupying nearly half of the autotomy segment. As in *L. sicula* the caudal vein contains a series of valves, each lying slightly in front of the corresponding vertebral split (Fig. 2). The effect of these valves, like that of the arterial "sphincters" would be to prevent undue loss of blood after autotomy.

## DISCUSSION

### 1. SIGNIFICANCE OF THE FAT LAYER

Most, if not all of the autotomous lizards described, and a few non-autotomous ones such as the Gila monster (*Heloderma suspectum*) possess a submuscular fat layer. This caudal fat is thought to provide a reserve of food. In *Lacerta vivipara* it is utilised during or just after hibernation (Avery, 1970), while in certain geckos and in the Gila monster it is drawn upon when the animal shelters from the rigours of a semi-arid habitat (Bogert and Del Campo, 1956).

The adaptive value of autotomy, as Etheridge points out, is very high and seems to be more important in many lizards than the benefit of storing fat in the tail. The fact that a caudal fat layer, divided by septa into transverse segments and longitudinal bands, appears to be characteristic of autotomous lizards even suggests that the fat may play some part in the mechanism of autotomy, quite divorced from its nutritive function. This idea is strengthened by the absence of caudal fat in non-autotomous forms such as the monitors (*Varanus*) and agamids such as *Calotes* (Woodland, 1920; Ali, 1949), but further work on biomechanical lines is needed to clarify this problem.

### 2. MECHANISM OF AUTOTOMY

Although autotomy may be facilitated by the mechanical strain exerted by a predator, it normally seems to involve active contraction of the tail muscles to a greater or lesser extent. These muscles have two distinct functions; to produce normal flexion of the tail, and to bring about autotomy. Their precise actions during the latter process can perhaps only be elucidated by electrophysiological methods; we were able, however, to draw certain inferences from the present study.

Our film shows that when the tail is grasped by forceps, the regions in front of and behind the point of seizure frequently contract strongly; sometimes the distal part of the tail writhes violently. Flexion of the tail in front of the forceps often takes place in both the lateral and vertical (dorsi-ventral) planes; the two movements are often combined to produce a rotatory effect. Here our observations differ from those of Woodland who found that in geckos only lateral flexion was important. By fixing the tail at one point the forceps act as a fulcrum for leverage; in some cases the tail was actually twisted around the forceps. The fixation of the tail probably helps to concentrate the stress at one particular fracture plane. Under natural conditions a comparable fixed point would be provided by the jaws or paw of a predator.

In most cases the fracture occurred at the front of the autotomy segment which was being held; it never took place more than three segments anterior to this. The economical character of autotomy, in which only a minimal portion of tail is usually shed, has been noted by previous workers.

Both Woodland (1920) and Boring *et al.* (1948) suggested that in geckos successive contraction of the muscles on two opposite sides of the tail is necessary to complete autotomy. Similar to-and-fro movement seemed to occur in a few of the autotomies observed by us in *Lacerta dugesii* (Fig. 4C). In the majority of cases filmed, however, the autotomising region of the tail seemed to be bent in one main direction only; to one side (Fig. 4A), or up or down, or in a rotatory fashion. (Fig. 4B).

The skin is first split on the stretched, convex aspect of the tail and then the muscles on this aspect separate from their weak anterior attachments. The split then appears to travel right across the remaining tissues of the tail. Separation of the two halves of the vertebra would require little force because of the presence of the fracture plane; separation of the fat segments on both sides would also be easy because the intra-adipose part of the autotomy septum consists of two layers with a potential plane of cleavage between them. It is perhaps more surprising that the skin and full thickness of the muscles on the concave, flexed aspect of the tail should also readily be divided by unidirectional bending without to-and-fro movement. It is possible either that such movement does occur but that the amplitude of the second contraction is so slight as not to be easily discernible in our film (except in a few cases); or else that the final rupture of the more superficial tissues on the concave aspect is effected by direct or rotational stress rather than by contralateral flexion.

Woodland and Boring *et al.* believed that the muscular contraction involved in autotomy is limited to a single segment only. This seems improbable, especially if to-and-fro movement is postulated. If the muscles on the stretched convex side of one segment are initially pulled away from their attachments they would be unable to contract effectively to produce a second flexion in the opposite direction. It is possible to envisage an alternative and more complicated mechanism in which the muscles are separated, not by stretching but by the force of their own contraction. We think it more likely, however, that several muscle segments are involved on one or both sides, and that if to-and-fro movement is necessary the intact segments adjacent to the ruptured one bring about the second contraction.

Woodland found that autotomy only occurred if part of the tail was fixed in some way. Nevertheless, it has occasionally been recorded in some species without the tail actually being touched; we have observed this once in *Lacerta dugesii*. It is possible that in such cases some irregularity of the ground or some feature of the surroundings would offer the necessary resistance to serve as a fixed point of leverage. Whether autotomy can ever occur if the tail is completely free remains uncertain.

### SUMMARY

1. The anatomy of the mid-caudal fracture planes of *Lacerta vivipara* is described, with special reference to the muscles and connective tissue septa. The presence of valves along the caudal vein is a feature of interest.

2. The role of the muscles in producing autotomy is discussed, partly on the basis of a film of induced autotomies in *Lacerta dugesii*.

We are grateful to Mr. David Rodgers of the Photographic Department, St. Mary's Hospital Medical School, for his great assistance in preparing the film, and to Mr. Barry Martin for skeletal preparations. This work was assisted by a grant from the Science Research Council.

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## ABBREVIATIONS

- an.n.sp, anterior neural spine  
 a.sep, autotomy septum between muscles (one-layered)  
 a.sep.b, autotomy septum through fat (two-layered)  
 c, centrum  
 c.a, caudal artery  
 cav, cavity into which muscle process fits  
 chev, chevron bone  
 c.v, caudal vein  
 d, dermis  
 d.f.b, dorsal fat band  
 d.m.l, dorsal midline  
 d.sep, dorsal part of median longitudinal septum  
 dura, dura mater  
 e, epidermis  
 ep.m, epaxial muscle  
 f, fat band  
 fr.pl, vertebral fracture plane  
 h, hinge of scale  
 h.sep, horizontal longitudinal septum  
 hy.m, hypaxial muscle  
 i.c.j, intercentral joint  
 i.v.p, cartilaginous intervertebral pad  
 l.s.r, long scale row  
 ma, marrow cavity of vertebra  
 n, n.c, nerve cord  
 per, periosteum  
 po.n.sp, posterior neural spine  
 sc, scale  
 sph, "sphincter" of caudal artery  
 s.s.r, short scale row  
 tr.p, transverse process  
 val, valve in caudal vein  
 v.f.b, ventral fat band  
 v. sep, ventral part of median longitudinal septum  
 w, plane of weakness in dermis  
 z.p.j, zygapophysial joint  
 1,3,5, anterior processes of epaxial muscle  
 7,9,11, anterior processes of hypaxial muscle  
 2,4,6, posterior processes of epaxial muscle  
 8,10,12, posterior processes of hypaxial muscle.

FIGURE 1.

Diagram showing relationships of muscles and vertebrae in mid-caudal region of *Lacerta vivipara*, seen from right side after removal of skin (c.  $\times 15$ ). The muscles of a single autotomy segment are shown. Attachments of muscles to vertebrae indicated by \*. The line DD shows plane of transverse section in Fig. 2D.

*Long broken lines*: outer surface of muscle, normally in contact with dermis. *Short broken lines*: outline of vertebrae, concealed by muscles. *Slanting lines*: Interlocking surfaces of muscle processes; these are covered by the autotomy septum.

Abbreviations on p. 285.

FIGURE 2.

Diagrammatic vertical longitudinal section through middle part of tail of *Lacerta vivipara*, slightly to one side of midline. (c.  $\times 25$ ). Arrows indicate points where skin breaks at autotomy.

Abbreviations on p. 285.

FIGURE 3.

A, B, C: *Lacerta dugesii*. A, tail stump after autotomy. B, proximal end of tail fragment after autotomy. C, one autotomy segment seen from above, showing scales, and muscle processes projecting behind and in front of the segment, after autotomy (All c.  $\times 10$ ).

D, E: *Lacerta vivipara*. D, transverse section through middle of tail in region of the autotomy plane (c.  $\times 10$ ). Interlocking muscle processes of segment in front in slanting lines; of segment behind in stipple. E, single epaxial muscle segment seen in oblique lateral view after removal of skin: diagrammatic. Outline of concavity between muscle processes in short broken lines. Longitudinal septa shown in long broken lines. Cav. 3 and cav. 5; cavities for processes 3 and 5 of muscle segment behind.

Abbreviations on p. 285.

FIGURE 4.

Diagrams illustrating methods of autotomy when tail is fixed. A, by lateral flexion in one direction (i and ii show successive phases). B, by flexion and rotation. C, by successive flexions (i and ii) in opposite directions (to-and-fro movement). Dorsal midline shown in broken lines. Forceps (tips only in A and C) are in black. Arrows show directions of bending.

# SITE TENURE AND SELECTION IN THE AFRICAN GECKO

*TARENTOLA ANNULARIS* (GEOFFROY).

by

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In an artificial "room", geckos sheltered most often behind "pictures" providing the greatest security. Despite an abnormally high population density, there was a significant tendency for each "picture" to be occupied only by a single gecko, indicating a degree of spacing. Individual geckos tended to occupy the same sites in many successive observations. "Pictures" lying horizontally on the floor were preferred to "pictures" hanging on the "walls". The attraction of the pictures was apparently due to the concealment they provided and not to the reduction in light intensity afforded. A "field" experiment confirmed the existence of site tenure and indicated a very slow rate of recolonisation in nature.

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## INTRODUCTION

Territorial behaviour is not uncommon among reptiles and has been recorded in *Testudines*, *Crocodylia*, snakes and lizards. Social organisation, resulting from aggressive interactions, is characteristic of *Iguanidae* and *Agamidae*. It varies in degree between species and according to ecological requirements (Carpenter, 1967; Rand, 1967). The males of many species of lizards appropriate territories for themselves and their females, from which invading males are driven off (*see* Bellairs, 1968, 1969).

Gekkonid lizards do not guard their eggs, nor do they exhibit parental care of the young (Kluge, 1967). According to Bustard (1965), however, males of the Australian gecko *Lucasius damaeus* Kinghorn show territorial behaviour, chase other males and occasionally fight. These fights are accompanied by a continuous chirping noise. *Diplodactylus vittatus* Gray also has a well-developed threat display, raises itself from the ground by extending its hind legs and inhales. Male *Gehyra variegata* (Dum. & Bib.) are territorial throughout the year, commonly sharing a tree stump with two or three females but driving other males away (Bustard, 1868a, 1969).

There is a definite limit to the number of *G. variegata* which can inhabit an artificial tree stump with a single male. This limitation results from social interaction between resident and non-resident females. It is not affected by food supply, but shows seasonal variations in intensity (Bustard, 1970). Territorial behaviour likewise continues throughout the year in both sexes of *Heteronotia binoei* (Gray). Males are seldom found in the same pile of bark unless the area is very extensive, although there may be several females and young present (Bustard, 1968b). To some extent the two species compete for home sites with one another and with *Oedura ocellata* Boulenger but, because of different preferences over food and microclimate, this competition is greatly reduced (Bustard, 1969).

The African house gecko *Tarentola annularis* (Geoffroy) has been claimed to be so aggressive that it is impossible to keep two males in the same cage on account of the resulting fights. They are said not only to injure their own jaws, but the bites they inflict on their opponents swell with blood and become septic (Grys, 1899; Loveridge, 1947). I have never observed any fight among many animals kept in captivity although, as mentioned by Kuntze (1932) and Cottam & Cottam (1923), these geckos bite very readily when handled. Sometimes, too, they express their objections vocally.

Casual observation has shown that individuals of this common domestic species tend to occupy the same locality over extended periods of time, indicating some degree of site tenure, although their behaviour could scarcely be described as territorial. The object of the work outlined below has been to investigate site tenure and selection in *T. annularis* outside the breeding season.



## METHODS

In the houses of Khartoum and Omdurman, *T. annularis* not infrequently takes refuge behind pictures hanging on the walls. An artificial "room", measuring 50 x 165 cm and 60 cm in height, was therefore constructed of hardboard. The floor was covered with sand and the top enclosed with fine wire netting. Four artificial "pictures" were hung at regular intervals, two on each of the longer walls of the "room". They consisted of mahogany blocks, 15 x 15 cm and 2.5 cm thick. Two screws were inserted, one in each of the upper back corners, so that they tilted forwards like pictures do. There were therefore spaces behind them in which the geckos were able to shelter.

In some experiments 8, in others 10 large geckos of both sexes (in the size range 20-80 g) were maintained in the "room", provided with a Petri dish of water and given cockroaches for food. This is an abnormally high population density. The positions of the geckos behind the "pictures" and on the walls were noted at irregular intervals up to five times daily over a period of five months (Nov. 1970-March 1971) after the end of the breeding season. Observation disturbed the animals greatly so that they left their refuges behind the "pictures" and darted about the "room" for a minute or two. However, since the intervals between counts were never less than 1 h., the geckos had invariably settled down again long before the following count.

In order to determine whether a "preference" was shown for horizontal or vertical sites, two of the "pictures" were placed on the floor in an area from which the sand had been swept away so that the hardboard surface beneath them was the same as that behind the "pictures" on the "wall". Experiments were also carried out in which one of the wooden "pictures" was replaced by a square of transparent "perspex" of similar size, to determine whether the attraction of the "pictures" was due to the darkness behind them or to the fact that they provided concealment. Concealment without much reduction of light intensity behind the "perspex" "picture" was afforded by hanging a thin sheet of white paper across the front of it.

A field investigation was conducted concurrently with the laboratory experiments in my concrete garage in Sharia el Barlaman, Khartoum. This was emptied except for some planks leaning against the west wall just inside the door, and some others at the back. These provided refuges behind which the resident geckos dashed for cover every time the door was opened. These geckos were then removed, as described below, and observations made at irregular intervals to see how quickly the garage was recolonised from elsewhere.

Some of the geckos could be recognised individually, others were marked by tying loops of string round one or more of their limbs. These identification tags were not easily distinguishable however, and the geckos were able to remove them after a few days.

## RESULTS

## DISPERSAL

When four "pictures" were available, occasionally two or more geckos would be found beneath the same "picture". More often, however, each "picture" was occupied by a single gecko, the remainder resting on various parts of the wall during the daytime. At night, the geckos left the "pictures" and wandered about on the "walls", immediately darting under cover of the "pictures" if the light was switched on. When disturbed during the day, the geckos in the open on the "walls" also frequently ran under the occupied "pictures". Then either they, or the original occupants, quite often dashed out again.

The results obtained are given in Table 1. They were analysed statistically to determine:

(a) Whether the animals showed preference for, or avoidance of, any particular "picture". If they were equally likely to go under A, B, C or D, the expected

Table 1. Position records of 8 geckos behind the various "pictures" (total, 526) and on the walls of the "room" (total, 274) (100 observations).

"Pictures"		No. of animals per "picture"					Total	
		0	1	2	3	more		
A	Observed	5	58	29	7	1	141	} $\chi^2_{[2]}$
	Expected	21.2	36.3	27.2	15.3			
B	Observed	5	31	49	15	—	174	} $\chi^2_{[2]}$
	Expected	14.1	31.3	30.4	24.2			
C	Observed	6	82	12	—	—	106	} $\chi^2_{[1]}$
	Expected	32.1	39.2	28.7				
D	Observed	12	71	17	—	—	105	} $\chi^2_{[1]}$
	Expected	32.4	39.2	28.4				
Total		28	242	107	22	1	526	

number beneath each "picture" would be  $526 \div 4 = 131.5$ . In fact the distribution was significantly different from this ( $\chi^2_{[3]} = 24.7$ ;  $P < 0.001$ ). "Picture" B was the most favoured, probably because it was furthest from the door of the laboratory and provided the greatest security. "Pictures" C and D were on the "wall" nearest to the door and consequently the geckos behind them received less warning before they were overlooked.

(b) In view of the conclusion reached above, it was necessary to analyse separately the position records of each "picture" to determine whether the probability of finding any one animal under a "picture" was independent of the position of other animals in the trial. Now the best estimate of the probability ( $P$ ) of an animal going under "picture" A is 0.17625, and the probability that it will not be under A is 0.82375. Similar reasoning can be applied to "pictures" B ( $P = 0.2175$ ), C ( $P = 0.1325$ ) and D ( $P = 0.13125$ ). The observed numbers of geckos under each picture in 100 trials is given in Table 1, along with the expected numbers for random distribution. In each case there is a highly significant difference ( $P < 0.001$ ) between observed and expected. This indicates that when the "pictures" are considered one at a time the numbers of animals beneath them are not what the binomial distribution would predict. From Table 1 it can be seen that the tendency is for there to be only a single gecko beneath each "picture" at any one time, despite the high population density in the "room".

When the entire "room" was rotated with reference to the laboratory, so that "pictures" A and D, and B and C were interchanged, the new "B" was the most highly "preferred".

Consequently, it must be concluded that *T. annularis* shows over-dispersal (that is, the geckos tended to be distributed evenly between the "pictures" without aggregating). This may have been a result of weak territorial behaviour, or else that sites already occupied tend to be avoided by other geckos without any defensive behaviour on the part of the occupants.

#### SITE TENURE

There was some tendency for individual geckos to occupy the space beneath the same "picture" in successive observations, as occurs under natural conditions in houses, and in the field experiment (p. 291). The geckos on the "walls" also tended to aggregate in one corner of the "room". This was near "picture" B, furthest away from the entrance to the laboratory. In 100 observations, 273 position records were obtained from this corner of the "room", compared with a total of 110 position records elsewhere (excluding records behind the "pictures"), when the "room" contained 10 geckos. One marked individual was observed in the corner near "picture" B on 24 occasions, in the opposite corner 29 times, and elsewhere on 20 other occasions. Less extensive but comparable data were obtained for site tenure by marked geckos underneath the various "pictures".

## PREFERENCE FOR HORIZONTAL SITES

A series of experiments was carried out in which the geckos were offered a choice of two "pictures" (B and C), one hanging on each of the longer "walls" of the "room", and two (A and D) lying on the centre of the "floor". The results obtained are given in Table II and show a highly significant

Table 2. Position records of 10 geckos behind the various "pictures" (total, 344) and on the walls of the "room" (total, 256) (60 observations).

No. of animals per "picture"	"Pictures" on walls		"Pictures" on floor	
	B	C	A	D
0	3	20	0	3
1	44	29	21	23
2	13	12	28	23
3	1	1	12	6
4	—	—	—	1
5	—	—	—	1
6	—	—	—	1
Total	73	56	113	102

"preference" for the "pictures" on the "floor". Whereas there is no significant difference between the total number of animals under "pictures" A + D and B + C ( $\text{Chi}^2_{[1]}=2.198$ ;  $P>0.1$ ) in Table I, there is such a difference in Table II ( $\text{Chi}^2_{[1]}=21.500$ ;  $P<0.001$ ). In this experiment "picture" B was again preferred to "picture" C.

## CONCEALMENT

The attraction of a transparent "perspex" "picture" was compared with that of the normal wooden ones with the following results (Table III). These show that the number of geckos sheltering behind the transparent "picture" was very much less than the number behind the normal wooden "pictures" although the former was in position B, normally the most highly favoured.

Table 3. Position records of 8 geckos behind the various "pictures" (total, 288) and on the walls of the "room" (total 272) (70 observations).  
"Picture" B was transparent, the others wooden.

No. of animals per "picture"	"Pictures"			
	A	B	C	D
0	2	55	2	20
1	24	15	40	45
2	32	2	25	5
3	9	—	3	—
Total	115	19	99	55

When a single transparent "picture" was provided and all the wooden ones removed, this was occupied by a single gecko only on 11 occasions out of a total of 25 observations on eight geckos.

When the transparent "picture" was covered with thin white paper, however, no significant difference was noted in the number of geckos hiding behind it (total 52) and behind the other three "pictures" (total 152) (geckos



on walls 148: total number of observations on eight geckos, 44). Since the amount of light behind the covered transparent "picture" was very much greater than behind the opaque wooden ones, it is probable that the important factor provided by the shelter of the "pictures" was concealment from view, not reduction in light intensity.

This conclusion was supported by the fact that when the white paper was hung diagonally across the transparent "picture" the geckos readily sheltered behind it, orienting their bodies so that they were entirely hidden from view by the paper.

#### RECOLONISATION OF VACANT SITES IN NATURE

Removal of geckos from a concrete garage and its subsequent recolonisation were recorded as follows. Unless stated to the contrary, the geckos were unmarked and can therefore be regarded as recruits apart from the easily recognisable large and small individuals left from the original population.

##### 1970

- 18 Nov 5 large geckos found and removed.
- 19 Nov 3 large and 1 small geckos found; 2 large geckos removed.
- 20-23 Nov No geckos found.
- 24 Nov 1 large gecko behind planks by door; 1 small gecko behind planks at the back.
- 25 Nov No change.
- 26 Nov 1 large gecko behind planks by door.
- 28 Nov-4 Dec No geckos found.
- 5 Dec 1 small gecko behind planks at the back.

##### 1971

- 3 Jan No geckos found.
- 4 Jan 1 baby gecko behind planks at the back.
- 5 Jan-4 Feb No geckos found.
- 5 Feb 1 large gecko behind planks by door.
- 9 Feb 1 baby gecko behind planks at the back.
- 11 Feb 1 large gecko behind planks by door.
- 12 Feb 1 baby gecko behind planks at the back.
- 13 Feb No geckos found.
- 18 Feb 1 large marked gecko released in garage.
- 20 Feb 1 large gecko behind planks by door.
- 21 Feb 2 large geckos and 1 marked large gecko behind planks by door.
- 23 Feb 1 marked and the new large gecko behind planks by door.
- 25 Feb No geckos found.
- 4 March 2 large geckos and 1 marked large gecko behind planks by door.
- 10 March 1 marked and the new large gecko behind planks by door.

These observations show that, in a period of four months, total recruitment to the garage (from which seven out of a total of nine geckos had been removed) was only by one large and one baby gecko. Throughout this period, the large and small geckos that had not been removed were always found in the same sites when present. Both recruits and the marked gecko that had been released, were likewise always found in the same sites when they were present in the garage. I do not know where the geckos disappeared to on the occasions when I did not find them, but there were one or two cracks in the wall which they might have entered and they could easily crawl underneath the door.

The above results confirm the existence of site tenure in *T. annularis* and indicate a very slow rate of dispersal to new sites in nature.

## ACKNOWLEDGEMENT

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## SUMMARY

The African house gecko *Tarentola annularis* (Geoffroy) frequently shelters behind pictures. It is not aggressive intraspecifically. Experiments carried out after the breeding season in an artificial "room" containing four almost equidistant "pictures" show that the gecko tended to select "pictures" that provided the greatest security i.e. those away from the door of the laboratory. Despite an abnormally high population density, there was a significant tendency for a single gecko to be found behind each "picture" at any one time, indicating either some degree of territorial behaviour, or else the avoidance of occupied sites. Individual geckos tended to occupy the same site in many successive observations.

"Pictures" lying horizontally on the floor were preferred to "pictures" hanging vertically on the walls. The attraction of the "pictures" was due to the concealment they provided and not to the reduction in light intensity they afforded.

A "field" experiment, carried out in an empty garage over a period of four months, confirmed that site tenure is manifested by these geckos, and indicated a very slow rate of dispersal to new sites in nature.

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THE DIET OF SOME JUVENILES OF THE COMMON TOAD (*Bufo bufo* L.)

By

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(Received 12/2/72)

The common toad (*Bufo bufo*) is stated to have an unselective method of feeding, taking any moving animal, limited only by size, available to it within its habitat (Smith 1951, Lescure 1964). The present paper seeks to investigate this view by detailing the gut contents of 16 young toads taken in pitfall traps, in an arable field during August/September 1969. A significant part of the potential prey fauna was known for this field.

## SAMPLING

A research project to study certain aspects of the crop fauna was carried out at the Haughley Research Farms, Stowmarket, Suffolk (N.G.R. 62/0.6.) during 1968-1970 (Paine, in preparation). Part of the project was routine monitoring sampling of the Coleoptera of nine arable fields (Harding 1971). Sampling during the crop growing season (April-May to harvest) was by means of pitfall traps containing either 2% Formalin solution or 25% Ethylene Glycol, as killing agent and field preservative. The toads taken in these traps were trapped fortuitously, and it should be emphasised that this technique and these killing agents are not advised for use in field studies on Amphibia.

The toads were trapped in one field which is divided into two sections. The west section (6 acres) was under "Fodder" crops (Turnips, Kale and Mangolds) with a narrow strip of Cabbages through the middle. The east section (5 acres) was under Field Beans. Records are divided into those taken from pitfall traps in either Beans, Fodders or Cabbages (Table 1). No pitfall trap was more than 200 metres from the presumed breeding site of the toads. The pitfall traps were in sample units containing different numbers and sizes of traps.

The juvenile toads were all in their first year, the adults having presumably spawned in a large moat, which surrounds a 16th Century manor house and lies along the south-western edge of the field studied. The average length of individuals (snout to urostyle) was 14 mm. Smith (1951) states that juvenile toads leave the breeding water between early May and late June. As these records date from 11th August to 5th September it is likely that these individuals had been living on land for approximately 1 to 2 months.

## GUT CONTENTS

Toads were dissected after being preserved for about 6 months in 70% alcohol. The stomach was removed with part of the duodenum and opened up. The mouth and throat were also examined. The entire contents of these organs from the 16 toads are listed in Table 1. Each gut contained a small quantity of unidentifiable animal fragments, some vegetable matter and soil. A percentage of the total number of individuals for each group of prey animals is given in Table 4. Numerically, Coleoptera comprised 64% of the prey animals. Parasitic Hymenoptera (12%) and Acari were present in every gut. No measure of biomass percentages was made.

## COLEOPTERA CONSTITUENT OF PREY

The only group of prey animals to be identified to species was the Coleoptera. A list of all the Coleoptera identified from the pitfall trap units which contained toads is given in Table 2. Of the 36 species taken in the 7 trap units, only 22 species can be considered to be potential prey animals to the juvenile toads (Table 2, Col 1): the remaining 14 species being too large and strong to be captured and ingested. Table 2 (Col. 2) shows that 13 of the 18 prey species also occurred in the relevant traps. Of these 13 species (76% of the prey Coleoptera—see Table 3), 10 species are of particular importance, as they make up 70% of the prey Coleoptera (Table 2). 9 of them belong to the Carabidae and Staphylinidae, both active, largely predatory families, and the other is the active pest weevil *Sitona lineatus*. Five species of Coleoptera, 24% of the total Coleoptera taken as prey, are not recorded in the pitfall traps, these are species which are not likely to be active on the soil surface. *Megasternum obscurum*, *Pselaphus heisei* and *Lathridius lardarius* are found in accumulations of decaying vegetation, *Phyllotreta nemorum* and *Ceuthor-*



DATE 1959	CROP	Beans		Cabbage			Fodders			Cabbage			Fodders			Cabbage			Fodders			Total
		11/8	1 2	22/8	3 4	5 6	7 8	9	22/8	29/8	10	11 12	13 14	15 16	29/8	11 12	13 14	15 16				
TOAD																						
COLEOPTERA																						
	<i>Bembidion quadrimaculatum</i>			2											1					4		
	<i>Trechus quadristriatus</i>								1						1		2			1		
	<i>Megasternum obscurum</i>	1		2	1			1		1					4		2		1	13		
	<i>Oxytelus rugosus</i>						1													1		
	<i>Tachyporus obtusus</i>																1		1	2		
	<i>Tachyporus</i> spp.			4			2	1												7		
	<i>Aleochara bipustulata</i>																			1		
	<i>Atheta</i> spp.																			1		
	<i>Pselaphus heisei</i>																			3		
	<i>Atomaria atricapilla</i>	1		1			2								1			1		4		
	<i>A. linearis</i>							1												1		
	<i>Atomaria</i> spp.					2														2		
	<i>Lathridius lardarius</i>							1												1		
	<i>Phyllotreta nemorum</i>							1	1											2		
	<i>P. atra</i> var. <i>cruciferae</i>																			1		
	<i>Longitarsus melanocephalus</i>																			1		
	<i>Sitona lineatus</i>	2	1	5	1	2	1	9	3		1		5	3	5		2	2		43		
	<i>Ceuthorhynchus contractus</i>						2			1										3		
	Coleoptera larvae						1										2	1	1	5		
HEMIPTERA																						
	Homoptera: Fulgoroidea			1	1						4		1		1					8		
	: Aphoidea																	1		1		
HYMENOPTERA																						
	Parasitica (+ many fragments)	1	2	2	1	1	1	1	1		4		2		1		1			18		
	Formicoidea						2	1												3		
COLLEMBOLA																						
	Arthropleona	2												1		1		1		5		
MYRIAPODA																						
	Chilopoda																1		4	5		
ARACHNIDA																						
	Araneae: Erigoninae	3	1						1									2		8+		
	Acari	P	P	P	P	P	P	P	P									P	P	P		

P = Present, quantity unknown.

Table 1. Analysis of gut contents of 16 juvenile Toads.

Species of Coleoptera taken in Pitfall Trap Units	3		
	1 Available as Prey	2 Occurrence in Gut	% of total Coleoptera in Gut contents
<i>Carabus violaceus</i> L.			
<i>Notiophilus biguttatus</i> (Fabr.)			
<i>Loricera pilicornis</i> (Fabr.)			
<i>Bembidion lampros</i> (Herb.)	+		
<i>B. quadrimaculatum</i> (L.)	+	+	4.2
<i>B. obtusum</i> Serv.	+		
<i>Trechus quadristriatus</i> (Schrank)	+	+	6.2
<i>Badister bipustulatus</i> (Fabr.)	+		
<i>Harpalus aeneus</i> (Fabr.)			
<i>H. rufipes</i> (Degeer)			
<i>Feronia cuprea</i> (L.)			
<i>F. melanaria</i> (Illiger)			
<i>F. madida</i> (Fabr.)			
<i>Calathus fuscipes</i> (Goeze)			
<i>Synuchus nivalis</i> (Panz.)			
<i>Oxytelus rugosus</i> (Fabr.)	+	+	1.1
<i>Euaesthetus bipunctatus</i> (Ljungh)	+		
<i>Lithocharis ochracea</i> (Graven.)	+		
<i>Lathrobium fulvipenne</i> (Graven.)			
<i>Xantholinus glabratus</i> (Graven.)			
<i>Mycetoporus splendidus</i> (Graven.)			
<i>Conosomus testaceus</i> (Fabr.)			
<i>Tachyporus nitidulus</i> (Fabr.)	+		
<i>T. chrysomelinus</i> (L.)	+	+	
<i>T. hypnorum</i> (Fabr.)	+		9.4
<i>T. obtusus</i> (L.)	+	+	
<i>Atheta</i> spp.	+	+	3.1
<i>Oxyptoda brevecornis</i> Steph.	+		
<i>Aleochara bipustulata</i> Erich.	+	+	1.1
<i>Ptomophagus subvillosus</i> (Goeze)	+		
<i>Atomaria</i> (spp.)	+	+	
<i>Phyllotreta undulata</i> (Kutsch)	+		
<i>P. atra</i> var. <i>cruciferae</i> (Goeze)	+	+	
<i>Longitarsus melanocephalus</i> (Deg.)	+	+	
<i>Psylliodes chrysocephala</i> (L.)	+		
<i>Sitona lineatus</i> (L.)	+	+	44.8

Table 2. Species of Coleoptera occurring in relevant pitfall traps and in toad guts.

*rhynchus contractus* are most commonly found on their food plants, which are various Cruciferae. The inefficiency of pitfall traps for sampling animals such as the above species, is well summarised by Greenslade (1964).

A	Number of species in traps	—	36
B	Number of species in guts	—	18
C	Number of species occurring in both guts and traps	—	13
D	Total number of individuals in traps	—	468
E	Total number of individuals in guts	—	96
F	Total number of individuals in C	—	73
	Numbers occurring in both guts and traps (F) as a percentage of total number in guts (E)	—	76%

Table 3. Numbers of individuals and of species of Coleoptera occurring in trap units and in toad guts.

	Haughley (1969)	Western France (1961-62)*
Coleoptera	64.4%	14.3%
Coleoptera larvae	3.4%	Not recorded
Hymenoptera parasitica	12.1%	Not recorded
Hymenoptera formicoidea	2.0%	62.9%
Hemiptera	6.1%	4.0%
Collembola	3.4%	2.3%
Myriapoda	3.4%	1.8%
Arachnida (Excluding Acari)	5.4%	5.2%

\* Comparable figures from Lescure (1964)

Table 4. Total prey animals—percentages for groups.

## DISCUSSION

Figures for the percentage composition of prey animals of adult toads have been given (Cott 1940, Theodorides 1953, and Lescure 1964). Their general conclusions were that toads prey predominantly on beetles and ants where these are available, but will take almost any prey that can be found. Guyétant (1967) studying young toads concluded that caterpillars, some Homoptera, millipedes, centipedes, slugs and snails were avoided by toads in their first summer.

The toads at Haughley were trapped in an arable field, a relatively poor habitat for invertebrates other than Coleoptera. The field was under an organic farming regime in which no artificial pesticides or fertilisers were used, so a large number of plant pests and their parasites were present, and the soil organic matter supported beetles such as *Megasternum obscurum* and *Pselaphus heisei*. The young toads were unable to reach far above the ground level, and hence were limited to prey available on the soil surface, within say 5 cms of the soil surface and in cracks and other irregularities in the ground.

The ten active common species of beetle indicated in Table 2 Col. 3 comprise 45% of the numerical total of prey animals but a higher percentage in volume. The remaining 55% of prey animals are composed of soil/litter dwelling animals and animals which would be fortuitously encountered by the toads.

It is worth noting that 44.8% (numerically) of the Coleoptera prey was *Sitona lineatus*, a common weevil feeding on Leguminosae. In some years *S. lineatus* has been known to cause considerable damage to Pea and Field Bean crops at Haughley. That as much as circa 50% of the biomass consumed by these toads was this pest species is a further indication of the beneficial function of toads.

## ACKNOWLEDGEMENTS

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THE VENOUS SYSTEM OF *AGAMA TUBERCULATA* GRAY

By

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(Received 14/9/71)*Introduction*

There have been extensive studies on the venous system of lacertids, geckonids, varanids, iguanids, amphisbaenids and scincids (Corti, 1847; Hochstetter, 1893; Beddard, 1904a, b, 1905, 1906; Bruner, 1907; Bhattacharya, 1921; Thapar, 1921; Mahendra, 1942; Sharma, 1954; Kashyap and Nigwaker, 1964). In marked contrast the veins of agamids are poorly known, although the family is well represented throughout the orient. The only detailed account of the agamid venous system is that of Bhatia (1929) on *Uromastix hardwickii*. However he omitted details of its cephalic veins, which were later described by Das (1960). Harris (1963) also described the circulatory system of *Agama agama*. An abnormal arrangement in the venous return from the oesophagus has recently been reported in *Agama tuberculata* (Raina and Duda, 1935). This present communication compares the venous system of *Agama tuberculata* with descriptions by Bhatia (1929) and Das (1960) on *Uromastix hardwickii* and by Harris (1963) on *Agama agama*.

## MATERIAL AND METHODS

Specimens were collected from Bhadarwah, Jammu and Kashmir State, India. Adults of both sexes (16 specimens in all), were chloroformed and dissected for gross observation. Injections with Reeves waterproof black Indian ink were made through the bases of the precavals and abdominal vein, which assisted minute observations.

## RESULTS

## THE POST-CAVAL VEIN (Fig. 1)

The thin-walled post-caval commences where the two efferent renal veins meet, via the transverse anastomosis. It is situated to the right of the median line in alignment with the right efferent renal vein, and runs forwards along the reflexed dorsal surface of the caudal extension of the right liver lobe, where it is partially embedded. Along its course it receives a vertebral vein from the area of the vertebral column and dorsal parietes. From the depths of the right lobe of the liver it emerges to open into the sinus venosus, curving to the right and following the curvature on the right side of the heart. While traversing the liver it receives a pair of hepatic veins (seen only after dissecting the right liver lobe), then an oesophageal vein and a dorsal and a ventral parieto-hepatic vein from liver mesenteries (Fig. 2).

Each efferent renal vein, from the hinder portion of the kidney, crosses the lumbar region and leads ventro-anteriorly to the kidney receiving 4-6 vessels from the latter and mesentery. The efferent renals join by the inter-renals—the posterior anastomosis. The two sub-equal efferent renal veins (the right slightly longer than the left) are separated by the dorsal mesentery. In front of the kidneys the efferent renals are situated mesial to the vasa deferentia (or oviducts) up to the testes (or ovaries). The left vein terminates here after receiving small tributaries from the left gonad, gonoduct and supra-renal (1 vasa from the genital duct; 1 adrenal from the supra-renal; 3 spermatic from the testis and 2 ovarian veins from the ovary). The left efferent renal joins the right via a single anterior transverse anterior anastomosis.

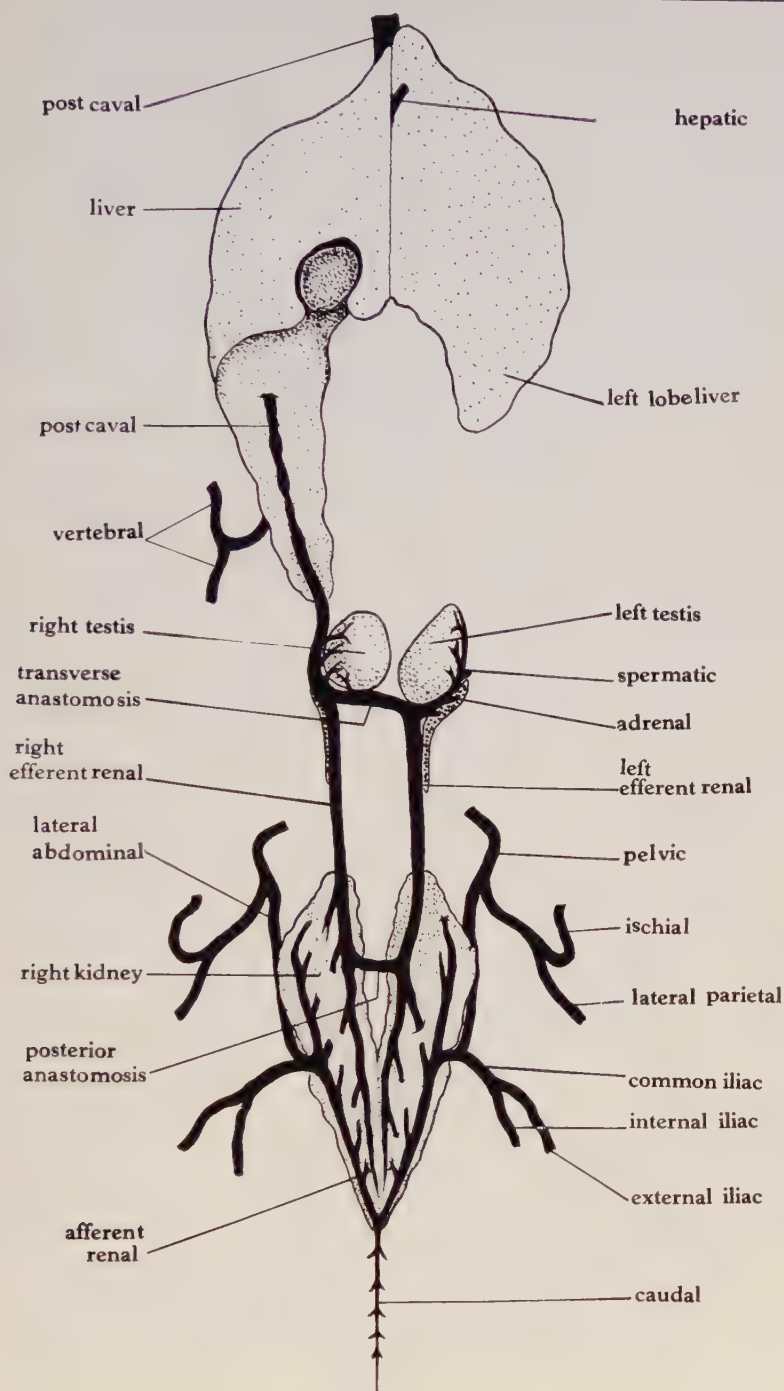


Fig. 1

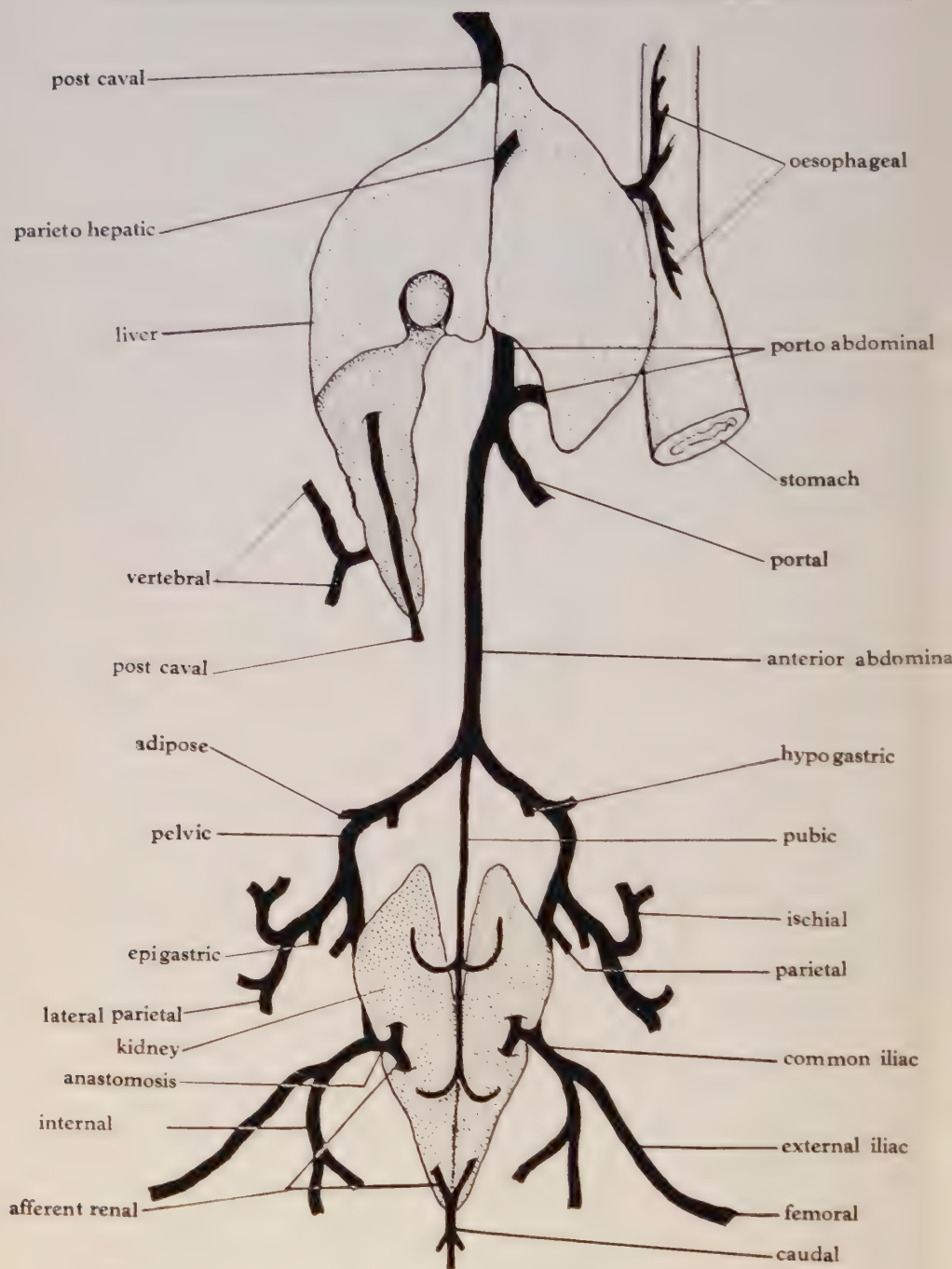


Fig. 2



On the right the latter receives an adrenal vein from the right supra-renal but only 1 of the 4 spermatic veins from the right testis. The other 3 open directly into the post-caval vein. In females a pair of ovarian veins open directly into the post-caval. The right vasa venosa opens into the right efferent renal vein.

#### THE RENAL PORTAL SYSTEM (Fig. 2)

The tail is drained by the caudal vein, which originates posteriorly and leads cranially through the haemal canal of the caudal vertebrae to the hind surface of the kidneys. It bifurcates into 2 afferent renals (= renal portal veins). The caudal vein receives tributaries from the caudal muscles. Each afferent renal connects via capillaries with the efferent renal of its own side. A short fairly large branch from the common iliac vein—the renal anastomosis (Fig. 2 see later anastomosis)—enters the kidney to meet the ipsilateral afferent renal vein and thereby establish direct connection between the afferent renal and abdominal veins.

The anterior abdominal vein originates in front of the pubic symphysis and is firmly attached to the abdominal musculature. It runs forwards midventrally to join the hepatic portal vein before entering the liver. Two pelvic and one pubic vein join to form the abdominal vein. The pelvic vein leads forwards dorso-laterally over the anterior half of the kidney, then turns ventrally along the anterior margin of the pelvis to unite in the mid-ventral line with its fellow of the other side. Each pelvic vein successively receives the parietal, lateral parietal, hypogastric and adipose veins. The small parietal collects blood from the posterior parietes above the kidneys, the large lateral parietal drains blood from the lateral abdominal musculature; it receives an internal vein from the rectum and an epigastric vein from the dorsal wall of the urinary bladder. The hypogastric vein drains the antero-ventral wall of the bladder. The adipose vein forms from small veins which drain the fat body and the pelvic vein traverses the latter.

A pubic vein originates behind the pubic symphysis from anterior and posterior symphyseal veins, which collect blood from the ventral musculature of the pubis and pubic symphysis. It leads into the abdominal vein.

#### THE HEPATIC PORTAL SYSTEM (Fig. 3)

The veins which drain the alimentary canal and together comprise the hepatic portal system are: the posterior intestinal, intestino-gastro-splenic, gastro-pancreatic and oesophageal veins.

The first three join at the portal vein and the fourth opens independently into the left lobe of the liver.

The long, stout posterior intestinal vein arises in the hinder intestinal region, by the confluence of a number of smaller intestinal veins. It joins a colo-caecal vein (formed by fusion of a caecal and 2 colic veins). The posterior intestinal vein then runs cranially, receives a stout rectal vein (formed from several smaller veins and a large cloacal vein) and then unites with the complex gastro-pancreatic and oesophageal veins.

The latter is formed by fusion of anterior intestinal, duodenal and gastro-splenic veins. The anterior intestinal vein originates near the posterior intestinal, from paired branches. It leads forwards and inwards to join the duodenal vein. The latter (formed by fusion of anterior and posterior branches) drain the duodenum. The gastro-splenic vein (formed by fusion of splenic and posterior gastric veins) originates dorsally at the front of the stomach. The posterior gastric (from dorsal anterior and posterior gastric vessels) drains the postero-dorsal region of the stomach. The gastro-splenic vein leads almost transversely and with the duodenal and the anterior intestinal forms the intestino-gastro-splenic vein, which continues forwards ventral to the pancreas to join the gastro-pancreatic vein—of the hepatic portal system.

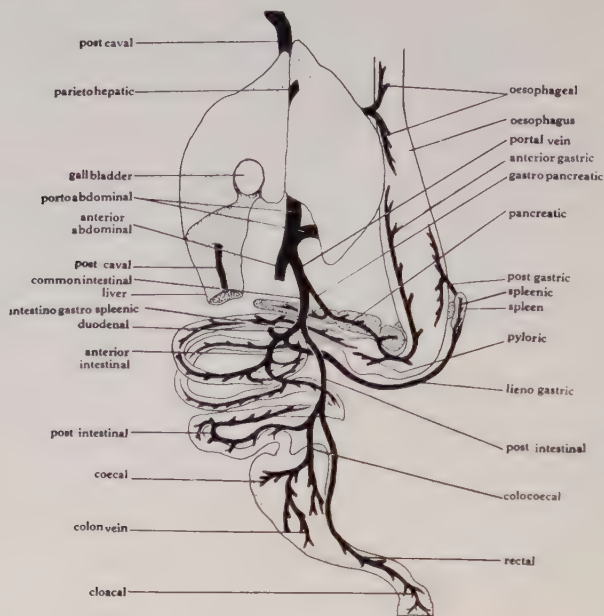


Fig. 3

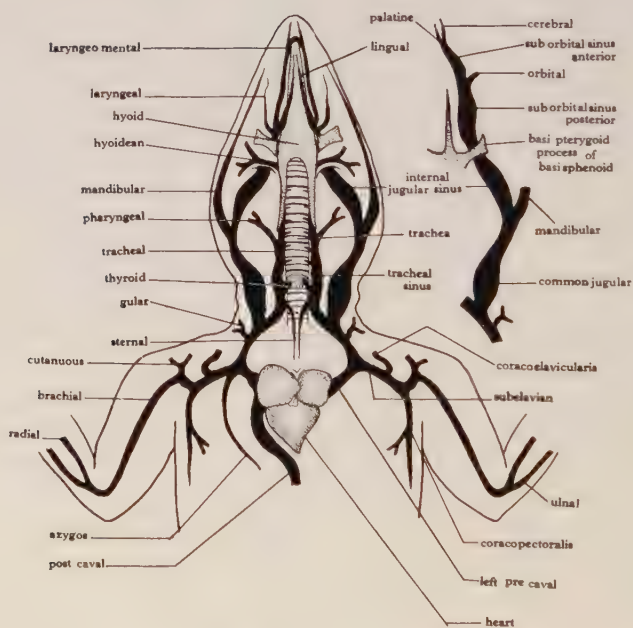


Fig. 4

The gastro-pancreatic vein forms from anterior gastric, pyloric and pancreatic veins. The large anterior gastric vein arises from the lower front surface of the stomach. It receives a small pyloric vein near the pyloric dilatation, and then passes to the pancreas. The pancreatic vein forms from a vein draining the part of the pancreas lying above the stomach, and another draining the pancreas in the duodenal loop. The former branch joins the common gastro-pyloric vessel near its entrance to the pancreas; the latter joins it at its point of emergence. The gastro-pancreatic vein emerges from the pancreas near the bile duct. It joins the combined trunk of the posterior intestinal and the intestino-gastro-linealis veins (Fig. 3), now called common intestinal vein, to form the large short hepatic portal vein.

The hepatic portal (Fig. 3, = portal vein) joins the anterior abdominal vein and eventually divides into 2 porto-abdominal veins, which enter the left lobe of the liver; the right porto-abdominal opens a little ahead and lateral to the left.

The oesophageal vein is former from anterior and posterior oesophageal veins, which join just before entering the liver. In the liver hepatic capillaries unite to form hepatic veins and a pair lead into the post-caval vein.

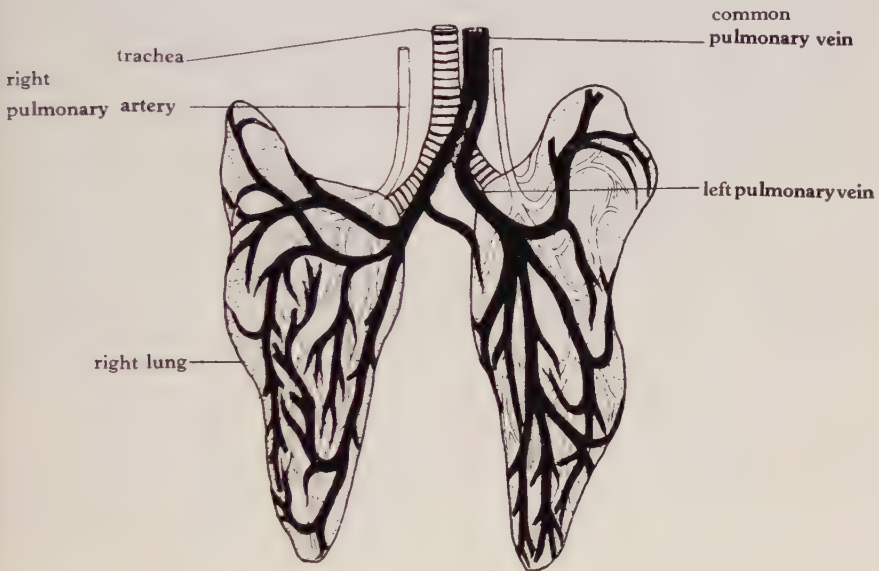


Fig. 5

#### THE PRE-CAVAL VEIN (Fig. 4)

The paired pre-cavals drain the head, shoulders, thorax, and fore-limbs. Each pre-caval is formed from the tracheal, common jugular and subclavian veins. The right pre-caval also receives an azygos vein.

The tracheal vein originates behind the lower jaw as a laryngeomental vein. Anteriorly the 2 laryngeomental (of each side) unite by a transverse hoof-like connection. Latero-caudally to the genioglossus muscle each one receives first a lingual vein from the tongue and then a laryngeal from the larynx musculature. The combined trunk runs dorsal to the epibranchiale and lateral to the trachea, to receive a hyoidean vein from the muscles of this



region. Thenceforth the trunk is the tracheal vein proper. It stays closely apposed to the middle third of the trachea and behind expands as the tracheal sinus. Two other prominent veins join the tracheal sinus, the thyroid and sternal veins. The former arises from a pair of small veins draining the thyroid; the latter drains the lower surface of the gular fold muscles and sternum. After receiving the sternal vein the tracheal sinus returns to about the same size as the tracheal vein and runs postero-laterally, to join the common jugular vein.

The common jugular vein receives the internal jugular and mandibular veins. The internal jugular (Fig. 4, inset), originates from the cerebral and palatine veins, the former draining the brain from numerous smaller vessels. The more ventrally situated palatine drains the upper palate including the organs of Jacobson. The paired palatines join mesially without forming a sinus. The internal jugular vein dilates antero-ventrally to the eye as the sub-orbital sinus anterior. An orbital vein from the eye empties into its hind end. The internal jugular dilates a second time postero-ventrally to the eye, into the sub-orbital sinus posterior, which narrows behind over the basipterygoid process of the basisphenoid, and thence lies over the palatine membrane in the hinder buccal cavity. Here the internal jugular dilates a third time as the internal jugular sinus. Nearer its termination the latter receives a small maxillary vein (not visible ventrally) from the upper jaw, muscles and skin. Behind, the internal jugular sinus meets the mandibular vein at the angle of the jaw.

The large mandibular vein drains the skin, muscles and mandible of its own side. The internal jugular joins it to form the common jugular vein, which widens into a common jugular sinus. The latter joins the tracheal vein to form a stout jugulo-tracheal vein, which receives a small gular vein draining the lateral neck muscles. The jugulo-tracheal vein turns slightly inwards to receive the subclavian vein. An elongate temporal vein from the auditory region opens into the common jugular sinus. It drains the middle ear and temporal region by the auricular and dorsal temporal veins. The long stout subclavian vein is derived from the brachial (*vide infra*), cutaneous, coraco-pectoralis and coraco-clavicularis veins, which in succession from behind forwards drain the fore-limbs, shoulders and pectoralis musculature. The smaller cutaneous vein drains the skin of the shoulder and muscles of the upper arm. It joins the brachial vein before the latter turns backwards and inwards to receive, on its post-axial surface, the coraco-pectoralis vein. The latter drains the postero-lateral region of the body. It originates within the pectoralis muscle, leads forwards to receive a short thick axillary vein and the combined brachial and cutaneous veins; the resulting massive vessel joins the small coraco-clavicularis (coraco-scapularis), which originates around the suprascapular cartilage. The coraco-clavicularis passes alongside the clavicle, recurves upon itself before combining with the other trunk to form the subclavian vein, which turns inwards and slightly backwards to join the jugulo-tracheal trunk and enter the sinus venosus as the pre-caval vein. The azygos vein runs dorsally along the right lung and receives two small veins from the thoracic vertebrae and a parallel series of smaller veins from the lateral thoracic parietes and sternal muscles.

#### THE LIMB VEINS

The venous return from the fore-limbs is from vessels at the bases of the digits. Pre- and post-axial vessels extend proximally as the radial and ulna veins. They drain the limb muscles and meet around the elbow as the brachial vein, which further proximally receives a pair of smaller veins from the ventro-lateral surface. The blood from the phalanges of the pes is collected by the femoral vein. On the under side of the thigh it receives veins from the thigh muscles to become the external iliac vein. The latter joins the internal iliac as they both leave the leg to form the common iliac vein.

The common pulmonary vein (Fig. 5) is short and arises from two fairly long pulmonary veins (one from each lung), which are closely apposed to each other, for a considerable distance, on the left of the trachea. Each pulmonary vein arises from 2 roots at the posterior half and one from the anterior half of the lung. The right pulmonary vein on leaving the lung turns left, lateral to the right bronchus, to receive a short vessel from the left lung.

### DISCUSSION

In *Uromastix hardwickii* the efferent renal veins originate from a "single sinus in the centre of the kidneys" (Bhatia, p. 16, 1929), in contrast to the intra-renal origin in *Agama tuberculata*. The latter is similar to *Lacerta* (Hochstetter, 1893), *Sphenodon* (O'Donoghue, 1920), *Hemidactylus* (Mahendra, 1942), *Varanus* (Sharma, 1954), *Agama agama* (Harris, 1963) and *Riopa* (Kashyap, et al, 1964). Younger specimens of *Uromastix* "exhibit a sort of anastomosis which becomes fused together in the adult, thus resulting in a prominent sinus" (Bhatia, 1929). This difference is therefore one of degree and the sinusoidal condition is basically of an intra-renal derivation. All lizards thus show an intra-renal origin of the efferent renals, except for *Pygopus lepidopus*, where the origin is post-renal (Beddard, 1904b).

*Agama tuberculata* differs from most lizards in the number of inter-renal vessels anastomosing between the two efferent renal veins. In *Sphenodon* there are 4 transverse vessels (O'Donoghue, 1929), in *Hemidactylus* there are 2 (Mahendra, 1942), but only one each in *Varanus monitor* (Sharma, 1954), *Lacerta* (Saunders and Manton, 1931, cited by Kashyap, 1964), *Agama agama* (Harris, 1963), *Riopa guentheri* (Kashyap, et al, 1964) and *Agama tuberculata*. *Agama* thus shows a higher grade of organisation than is the case with lizards having more than one anastomosing vessel, or a sinus in between.

In *A. tuberculata* and *A. agama* (Harris, 1963) the abdominal vein is single in contrast to the 2 abdominal veins in *Uromastix* (Bhatia, p. 25, 1929). The veins join only occasionally along their course. *Uromastix* may thus be unique among lizards in possessing this primitive arrangement.

In *Agama* the external jugular vein is missing, but has been reported in *Uromastix hardwickii* (Das, 1960) and *Varanus bengalensis* (Thapar, 1921). However in *V. bengalensis*, Mahendra (p. 241, 1942) showed that Thapar had mistaken the tracheal vein for the external jugular, which correction was confirmed by Sharma (1954) in *V. monitor* (= *V. bengalensis*). *Uromastix* alone among lacertilians therefore possesses an external jugular vein. Das (p. 80, 1960) states "that in *Uromastix* the lingual and mandibular veins part company . . . the maxillary and mandibular join to form a distinct vein, which must be considered as an external jugular vein". However Das disregards the fact that the external jugular vein either in amphibians (Gaupp, 1899; Bethge, 1898) or mammals (Salzar, 1895; Mall, 1904; Smith, 1909) forms by the confluence of the ipsilateral lingual and mandibular veins. Das' assumption therefore does not support the view that an external jugular exists in *Uromastix*. In *A. tuberculata* and *A. agama* the mandibular vein receives no factors until it meets the common jugular sinus; in *Uromastix* the maxillary vein is reported to join the mandibular before the latter opens into the common jugular sinus.

Reduction in the number of tracheal loops is a primitive condition (Mahendra, 1942). *Agama tuberculata*, *Hemidactylus* (Mahendra, 1942) and *Riopa guentheri* (Kashyap, et al, 1964) are therefore primitive in this respect and differ from *Uromastix* (Das, 1960), *Sphenodon* (O'Donoghue, 1920) and *Varanus* (Sharma, 1954).

The cranial sinuses of the jugular vein of *Agama tuberculata* do not depart from the typical saurian pattern, though their relative positions are slightly at variance with those recorded in other lizards. The absence of an orbital sinus in *Agama* is, however, characteristic. Possibly the space available in the orbit is not sufficient to accommodate such a large structure. In *Agama* there are only the suborbital sinus anterior and posterior. The presence of the former in close proximity to the olfactory capsule, might explain the absence in *Agama* of the sinus nasalis of *Varanus* (Sharma, 1954). The cranial sinuses of *Uromastix hardwickii* and *Agama agama* were not adequately described by Das (1960) and Harris (1963) respectively.

Although a vena cerebialis posterior is generally present in lacertilians (Grosser, *et al*, 1895; O'Donoghue, 1920), it was not found in *A. tuberculata* or reported in *A. agama* (Harris, 1963) and in *Uromastix* (Das, 1960). Its absence may be a feature of agamids.

The retention by *Agama* of an azygos, only on the right side, resembles the condition in *Phelsuma madagascariensis*, *Tarentola annularis*, *Heloderma suspectum* (Beddard, 1906), *Hemidactylus flaviviridis* (Mahendra, 1942) and *Riopa guentheri* (Kashyap, *et al*, 1964) but differs from that in *Iguana tuberculata* (Beddard, 1904a), *Varanus griseus* (Beddard, 1906), *Varanus monitor* (Sharma, 1954) and *Uromastix hardwickii* (Das, 1960), which possess paired azygos veins — a more primitive arrangement.

The hepatic portal system in *Agama* differs from that in *Uromastix*. The rectal vein in *Agama* is a constituent of the latter; it appears to be part of the renal portal system in *Uromastix* (see Bhatia, 1929). The posterior gastric veins in the two agamids are not identical. In *Uromastix* (Bhatia, 1929) it seems to be equivalent to the pancreatic vein of *Agama*, without its connection with the stomach.

The intestino-gastro-splenic vein forms from the posterior intestinal in *Uromastix* but from the anterior intestinal vein in *Agama*. Only the anterior and posterior gastric veins drain the stomach in *Agama* but these and the anterior dorsal gastric veins do so in *Uromastix*. However the anterior gastric vein in *Agama* follows a course comparable to that of the posterior gastric vein of *Uromastix*. On account of (a) its origin in front of the posterior gastric vein, (b) the absence of a second set of gastric veins below the stomach and (c) its entry into the pancreas through a pyloric dilation, it cannot be homologised with the posterior gastric vein of *Uromastix*. The author prefers to name this vein the anterior gastric vein.

In *Uromastix* the common intestinal vein passes above the duodenum, before entering the pancreas to join the posterior gastric vein (Bhatia, 1929). In *Agama* it passes below the duodenum to join the gastro-pancreatic vein outside the pancreas, so as to form the hepatic portal vein.

Finally in *Agama* the entrance of the portal vein into the liver is entirely different from the condition in *Uromastix* (Bhatia, 1929).

### CONCLUSIONS

(1) Agamids are similar to other lizards in that the efferent renals originate intra-renally. *Pygopus lepidopus* is an exception where the origin is post-renal. The sinusoidal origin in *Uromastix* is a specialisation of intra-renal derivation.

(2) There are from 1-4 constituent vessels of the inter-renal anastomosis in lizards. In agamids there is only one, which is probably a specialisation.

(3) The iliacs of agamids nearly always originate pre-renally.

(4) The external jugular vein is absent in lizards.

(5) There is only one tracheal loop in *Agama*, a primitive arrangement; and 4 loops in *Uromastix*, a specialised condition.

(6) *Agama* is characterised by the absence of an orbital and nasal sinus.



(7) The absence of a vena cerebialis posterior would seem to be unique for Agamidae.

(8) In agamids the veins of the hepatic portal system are the most variable of the venous system.

(9) In terms of the arrangement of the venous system *Agama* is generally more specialised than *Uromastix*; the latter retains paired abdominal and azygos veins (= epigastric veins of Das, 1960), more than one inter-renal anastomosing vessel and a symmetrical arrangement of the anterior veins. *Agama* is however less specialised than *Varanus*, *Pygopus* and *Chamaeleon*.

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#### EXPLANATION OF THE TEXT FIGURES. AGAMA TUBERCULATA

Fig. 1. The post-caval vein and renal portal system; ventral view.

Fig. 2. The anterior abdominal vein and its formation.

Fig. 3. The hepatic portal system: ventral view.

Fig. 4. The anterior veins and the formation of the pre-caval vein. Inset showing the formation of the internal jugular vein.

Fig. 5. The pulmonary veins: ventral view.

THE UNIQUE DEFENCE MECHANISM OF *RHABDOPHIS TIGRINA*  
(=*NATRIX TIGRINA*, COLUBRIDAE, OPHIDIA)

By

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(Received 18/12/71)

In 1935 the Japanese herpetologist K. Nakamura of the University of Kyoto published in the Memoirs of the College of Science of that University a detailed and well-documented description of structures he discovered in the nuchal region of a fairly common Japanese snake *Rhabdophis* (then known as *Natrix tigrina*). His discovery found its way into some of the more detailed textbooks by later authors (Angel, 1950; Bellairs, 1969) but many of the facts which he and a few later investigators (Smith, 1938; Fukada, 1958, 1961, 1964) brought to light, are still unknown to many present day herpetologists. A few specimens of this snake, which is rarely seen in Western collections, but made available through the kindness of Professor Fukada of Kyoto University and Mr. Nakagawa, Curator of the Ueno Zoo, Tokyo, suggested this review.

It is usually an easy matter to remove the skin from a small colubrid snake since it is only loosely attached to the muscular layer. In *R. tigrina* a resistance is encountered on both sides of the mid-line about 5 cm from the occiput. It seems that in the live snake, particularly if the skin in this region is stretched, the presence of sub-epidermal paired structures can be seen with the naked eye. In preserved material this is not possible and the skin can only be removed from this area by careful dissection. It then becomes apparent that the adherence of the skin to the muscle is due to connective tissue surrounding paired oval translucent structures of which, in the adult snake, there are usually 14, arranged in two parallel rows to both sides of

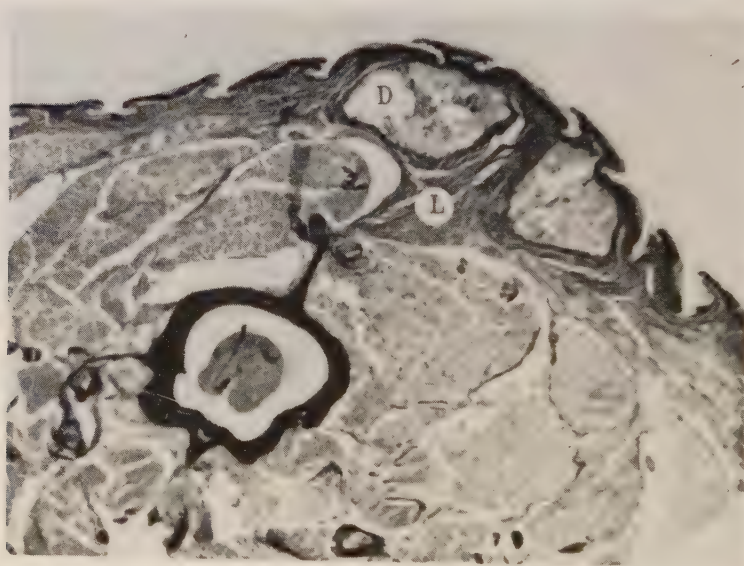


Fig. 1  
*Rhabdophis tigrina* Nuchal region, transverse.  
D, Dorso-nuchal gland; L, Nuchal ligament.



Fig. 2 *Rhabdophis tigrina*. Dorso-nuchal glands. Skin folded to accommodate on section.  
Scale: 1 mm. v. Gieson's stain.

the mid-line. In *R. tigrina* no more than 14 or 15 pairs of these structures are found, occupying only the neck. There have, however, appeared reports that in a very few other Colubrids similar organs extend all along the dorsal mid-line (Smith, 1938). In the absence of a better designation we shall refer to these structures as "glands" although it seems doubtful if, strictly speaking, their histological structure brings them into this category. They are small sacs, filled with a viscous, neutral, yellowish, unpleasantly smelling, slimy fluid but they have no excretory duct and the fluid only escapes if the nuchal skin is strongly bent or squeezed so as to cause a rupture of the thin epidermal lamella which separates the glands from folds between nuchal scales (Figs. 1 and 2).

In 1938 Malcolm Smith examined the majority of the snakes of the Indo-Chinese and Malayan region insofar as they were available in the collection of the British Museum of Natural History. Of the 45 species examined dorso-nuchal glands were only found in the following 10 species:

- Natrix* (now *Rhabdophis*) *tigrina* (Boie)
- Natrix subminiata* (Schlegel)
- Natrix himalayana* (Günther)
- Natrix nuchalis* (Boulenger)
- Natrix auchenia* (Smith)
- Natrix nigrocincta* (Blyth)
- Macropisthodon plumbicolor* (Cantor)
- Macropisthodon rhodomelas* (Boie)
- Macropisthodon flaviceps* (Duméril and Bibron)
- Balanophis ceylonensis* (Günther)



In his well-illustrated paper Parker showed that the structures in question do not always appear as a chain of paired separate glands but that, in the *Macropisthodon* group and in *Balanophis*, it looks as if the glands had become fused so as to form one single pocket, extending on both sides of the dorsal mid-line for about 1.5 cm. Nor are these glands always limited to the nuchal region as they are in *Rhabdophis tigrina*. In *N. nigrocincta* he counted 167 pairs of glands, distributed down to the caudal region; in *N. himalaya* there were 40 pairs of glands. Parker's views on the taxonomic value of these glands are guarded in view of the limits of his investigation, nor did his Museum material produce any very definite histological picture. It looks, however, as if the histology of the single and multiple gland structures is, if not identical, very similar.

Twenty years went by until Fukada (1958, 1961, 1964) explained the function of the dorso-nuchal glands from observations made on live material in Japan where *Rh. tigrina* is a common species. He reported that this snake rarely bites but, when in danger of capture, it rather tries to escape. In cool weather however, when the snake cannot move very fast, it flattens the body and arches the neck so as to stretch the dorso-nuchal skin which contains the glands. The epidermis of the scale pockets seems to represent a point of minor resistance because it breaks where normally it covers the glands and allows the contents to ooze out. Accidents where a drop of this fluid entered a human eye and experiments on frogs' tongues proved that secretion to be highly irritant and causing prolonged inflammation without however having any lethal effect. The effect however seems to be strong enough to deter any predator from swallowing the snake.

Fukada was furthermore able to show that these glands are not of ectodermal origin but that they derive from cells aggregating in the dermis where they can be detected in 10 day old embryos. He emphasised their mesodermal origin, that they have neither a lumen nor an epithelial lining and they only go into action when the snake is, or believes to be in immediate danger. He also reports that, on such occasions, the snake executes peculiar "twisting" movements with the head, the value of which it has not been possible to explain.

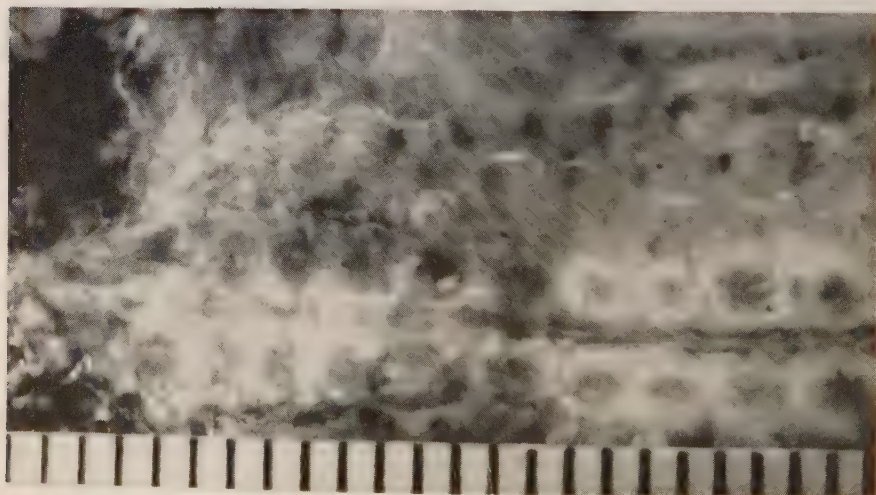


Fig. 3 *Natrix tigrina*. Dorso-cervical glands. Aspect of under side of skin. VIII/71. Scale: mm.

The largest diameter of the individual gland is 1.5-2.5 mm. Authors divide the reptilian dermis into an external "*corium laxum*" and an internal "*corium densum*". The glands occupy almost the whole thickness of the latter. The overlying *corium laxum* too is very thin where the glands occur, with the result that, in the scale-folds the glands are covered by the epidermis alone.

Sections show the histology of these structures to be very different indeed from what we usually designate as a "gland", be it exo- or endocrine (Fig. 3). Endocrine glands may have no excretory duct but they are, at least lined with some kind of epithelium. Both these items are missing in the structures under discussion. The "glands" have the structure of simple sacs, not lined by any cellular layer. Without a distinct wall they displace the collagenous fibres of the *corium densum*. But they are by no means empty. Numerous capillaries enter the sacs from the periphery. They divide and form a network of thin-walled blood-vessels traversing the lumen of the sac. Filling the meshes created by these capillaries lie the cells which produce the essential excretory product of the gland. Preserved material does not provide us with much information on the nature of this product. Frozen sections, stained with oil-red show innumerable lipid micro-granulae distributed in the capillary walls and everywhere in the intercapillary spaces (Figs. 4 and 5). These

Fig. 4

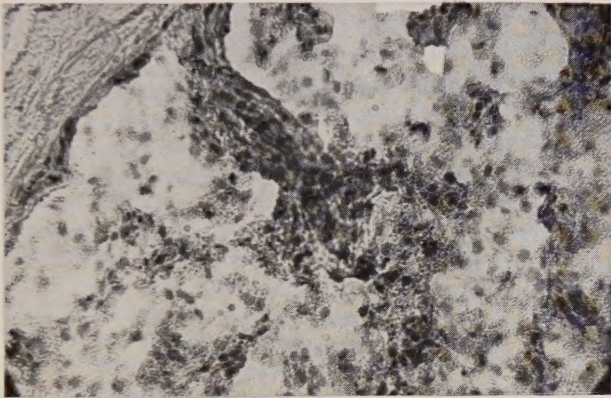
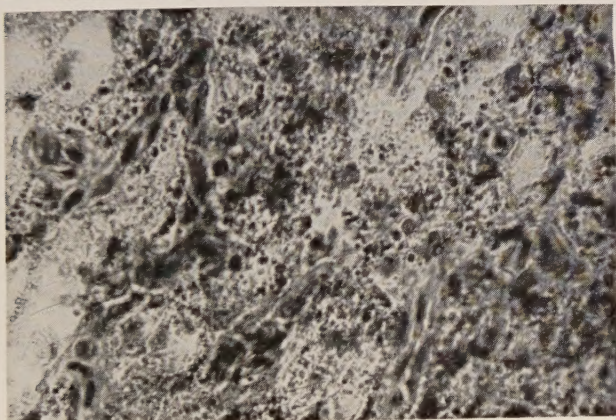


Fig. 5



*Rhabdophis tigrina*. Contents of dorso-nuchal gland at high magnification. Frozen section, stained with Oil red. Capillaries, nuclei and numerous very small fat droplets can be seen.



droplets do not take any other stain and they are P.A.S. negative. They are  $1\text{--}2\mu\text{m}$  thick and do not occur anywhere but in the lumen of the glands. They may, possibly be the carriers of the essential defensive substance produced by the glands. Importation of live snakes will have to await further elucidation of this problem. In the meantime, the majority of snakes have not yet been examined for the possession or otherwise of dorso-nuchal glands, a piece of research for other herpetologists.

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## NEW LOCALITY RECORDS FOR GREEK REPTILES

By

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(Received 29/9/71)

Between 1969 and 1971 I made numerous herpetological collections in Greece. Some species I believe are here recorded for the first time from certain island and mainland localities.

Island of Symi, near Rhodos, in the Dodecanese: *Testudo graeca iberica*, *Mabuya aurata*, *Coluber j. jugularis*, *Coluber ravergeri*, *Eirenis modestus*, *Vipera xanthina*.

Island of Tilos, near Symi. *C. j. jugularis*.

Island of Santorini (Thira), Cyclades: *Elaphe situla*.

Island of Agios Georgios, between Hydra and Cape Sounion: *Lacerta erhardii*, *Gymnodactylus kotschy*.

Island of Ipsili, Gulf of Argolis: *Testudo marginata*, *G. kotschy*, *Ablepharus kitaibelli*, *Lacerta peloponnesiaca*, *Algyroides moreoticus*, *Coluber gemonensis*, *Malpolon monspessulanus insignitus*.

Island of Plateia, Gulf of Argolis: *Lacerta trilineata*.

Island of Tolon, Gulf of Argolis: *T. marginata*, *Coluber najadum dahlia*, *C. gemonensis*.

Island of Velopoula (Parapola), 30 miles S.E. of Spetsai towards Milos in the outlying Cyclades: *Lacerta milensis*, *G. kotschy*.

Kalamata, southern Peloponnese: *Elaphe longissima*.

Remarks: Of particular interest is the presence on Ipsili of *L. peloponnesiaca* and I believe this to be the first record of this lizard on any island. The species has always been considered endemic to the Peloponnese.

In several years of collecting in Greece I have come across only two specimens of *E. longissima*—one from near Lamia on the east side of the mainland of central Greece and this specimen here recorded from the Peloponnese.

I also visited the Karavi islands, a group of three tiny islands lying 10 miles S.E. of Velopoula. These lie within the anticipated range of *L. milensis* which is endemic to the Milos group and the outlying islands of Velopoula and

Falconera. The largest of the Karavi islands has 100 foot vertical cliffs and appeared inaccessible. The smallest of the group is little more than a large above-water rock and is probably often awash. I managed to land on the other island which is about 30 feet above sea level, but found no sign of reptile life. This island, as I learned later, is used as a target by the Greek Navy and the rocky terrain is severely pounded. Any lizards that might have existed have evidently been exterminated. The largest island could still perhaps support a lizard population.

## ACKNOWLEDGEMENTS

I visited the islands of Agios Georgios, Ipsili, Plateia, Tolon, Velopoula and Karavi in my own locally built Greek fishing boat. All these islands are uninhabited and the trip would not have been feasible without assistance. I am indebted, therefore, to Mr. John Lloyd for accompanying me and for his invaluable help in obtaining specimens. I am also grateful to the owner of the motor yacht "Thistle"—Mr. Anthony Powell—for providing me with transport on my first visit to Velopoula.

## BOOK REVIEWS

SYNOPSIS OF THE HERPETOFAUNA OF MEXICO. Volume I. Analysis of the Literature on the Mexican Axolotl. By Hobart M. Smith and Rozella B. Smith. 1971. Eric Lundberg, West Virginia.

The Smith's have compiled a thorough bibliography of the literature on the axolotl (*Ambystoma mexicanum*), listing some 3,311 titles which include or pertain to this salamander. The bibliography portion is preceded by a 27 page introduction which includes such topics as "sources", "coverage", "application of the common name", "the proper generic name", "populational relationships", "specific and/or subspecific names", "the family name", "fixation of neoteny", "cause of transformation", "history of literature on the axolotl", "literary significance", "care", "economic value", and "analysis of the indices". It is concluded with an extensive subject index, followed by an index to co-authors and finally by an index of serial abbreviations.

The bibliography will be most useful to embryologists, anatomists and physiologists. However, the lengthy index of serial abbreviations (31 pages) will be most useful to many other zoologists and also to librarians.

KENNETH L. WILLIAMS

THE CASE OF THE MIDWIFE TOAD. By A. Koestler (1971). Hutchinson, London. £2.00.

The older generation of Biologists cannot yet have forgotten the tragic death of the Viennese zoologist Paul Kammerer who shot himself in 1926 at the end of a meteoric career from obscurity to great achievement and back to obscurity again. Probably his act of despair was not only due to his part in the contemporary vociferous conflict between the Darwinians and the Lamarckists; there may have been contributory reasons of a more private nature. The conflict however which his death brought to the knowledge of the public, still persists, and the recent Lysenko affair has shown how easily flames can again burst forth from Kammerer's funeral pyre. Koestler's book, obviously a labour of love, dedicated to a brilliant compatriot, is very much worth reading. He says there is no Kammerer biography, but English readers



have been told the story by W. Ley in 1955\*. This book however, is now out of print and we can only hope that biological scientists — and not these only — of today will take the opportunity of reading the cautionary tale of the rise and fall of one of the most gifted zoologists Austria has produced. Even after 46 years no authority has been able to prove whether Kammerer was quite right or quite wrong. Surely there must be an Institute of Zoology somewhere supplied with sufficient funds and devoted staff to repeat his experiments. That is: if they are repeatable.

E. ELKAN

\*Ley, W. (1955). Salamanders and other wonders. Phoenix House, London.

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